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MADROÑO

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CONCENTRATION OF ENVIRONMENTAL EXTREMES AS THE BASIS FOR VEGETATION AREAS

LEROY E. DETLING

Concepts of vegetation areas are ordinarily based upon some concept of endemism; that is, a geographical area whose flora contains a noteworthy number of species endemic to that area is thought of as a vegetational unit. These areas are usually given boundaries coinciding with major physiographic features, but the environmental features of the region enter only secondarily into the picture.

In a recent publication based upon a transect study in western and central Oregon (Detling, 1948) attention was called to the correlation existing between the percentage of endemism in the various vegetation belts and the degree of extremeness of environmental factors in those same belts. It was shown that where gradients of several environmental factors exist, those areas where the greatest number of extremes occur are the ones which show the highest percentages of endemism, while those areas along the gradient where the environment is most moderate are characterized by a relatively low degree of endemism.

This being true, it should hold that over any extensive geographical region those centers in which the extremes of a number of climatic or other environmental gradients occur together will be the centers of endemism as regards their flora. This should serve as a basis for dividing such a region into vegetation areas, each with its characteristic flora.

The present paper describes the procedure which has been followed in mapping such areas for the Pacific Northwest, and shows how the areas thus established are related to the distribution of a few of the dominant plant species.

The environmental factors upon which this investigation is based are all climatic features, viz., annual precipitation, average January temperature, average July temperature, and length of the period between the last killing frost in the spring and the first killing frost in the fall. These features in themselves may not always be what are most important as the limiting factors in the distribution of plant species, but they undoubtedly reflect those features which are the limiting factors. Seasonal distribution of rainfall may be of greater importance to plant life in some areas than the annual total, but in the geographical region under consideration the relative distribution of moisture among the seasons is fairly constant, no matter what may be the actual total precipitation. Again, the limiting factor for plants in winter temperatures is the actual lowest temperature that occurs, but it is found in comparing these lowest temperatures where they are available that they

vary from one locality to another directly as the average January temperature varies, and are thus reflected with sufficient accuracy in these January averages to make the latter valid for purposes of our comparative study.

The data used in this investigation are readily available in the annual reports of the United States Weather Bureau. The climatic maps are adapted from the 1941 Yearbook of the United States Department of Agriculture, "Climate and Man." Data on the climatic features which might have more direct bearing on the flora, such as those just discussed, are not available from a sufficient number of stations over as large an area as the Pacific Northwest, and to collect them would have been a task of too large proportions for one worker to undertake.

Edaphic factors are of great importance in determining the character of a flora. They frequently serve to explain local variations, or in some instances even form the basis for subdividing the major vegetation areas into smaller units, but climate still remains the chief basis upon which these major floras are determined, and for this reason edaphic conditions have not been included in this study.

The first step in the mapping procedure was to determine the gradients for each individual environmental factor. These are shown in the climatic maps of Figures 1 to 4. A cursory inspection of the maps is sufficient to reveal the location of the extremes of these gradients. Examples of extremes, either high or low, may be noted in the annual precipitation in the Olympic Mountains, in the Big Bend of the Columbia River, and at Pyramid Lake in western Nevada, in the average July temperature on the Oregon and Washington coasts, in the Rogue River Valley, and in the Big Bend of the Columbia River, in the average January temperature on the southern Oregon coast, the Cascade Mountain summits, and the lower Clearwater River in Idaho, and in the length of growing season on the southern Oregon coast and on the plateau of central Oregon.

The location of the more noteworthy of the gradient extremes for all four climatic factors is indicated in Figure 5. High extremes of temperatures and precipitation and the longest growing seasons are marked by solid dots, the opposite extremes by circles. The letters accompanying these marks indicate the climatic factors to which they appertain, as follows: P, annual precipitation; S, July (summer) temperature; W, January (winter) temperature; G, growing season.

When the extremes for all factors are mapped together in this manner it is noted that there are certain points around which they tend to be concentrated. According to the findings of the study previously referred to it is at these points that we should expect the highest degree of endemism. The next step, therefore, was to locate the major concentrations of extremes, which would serve as

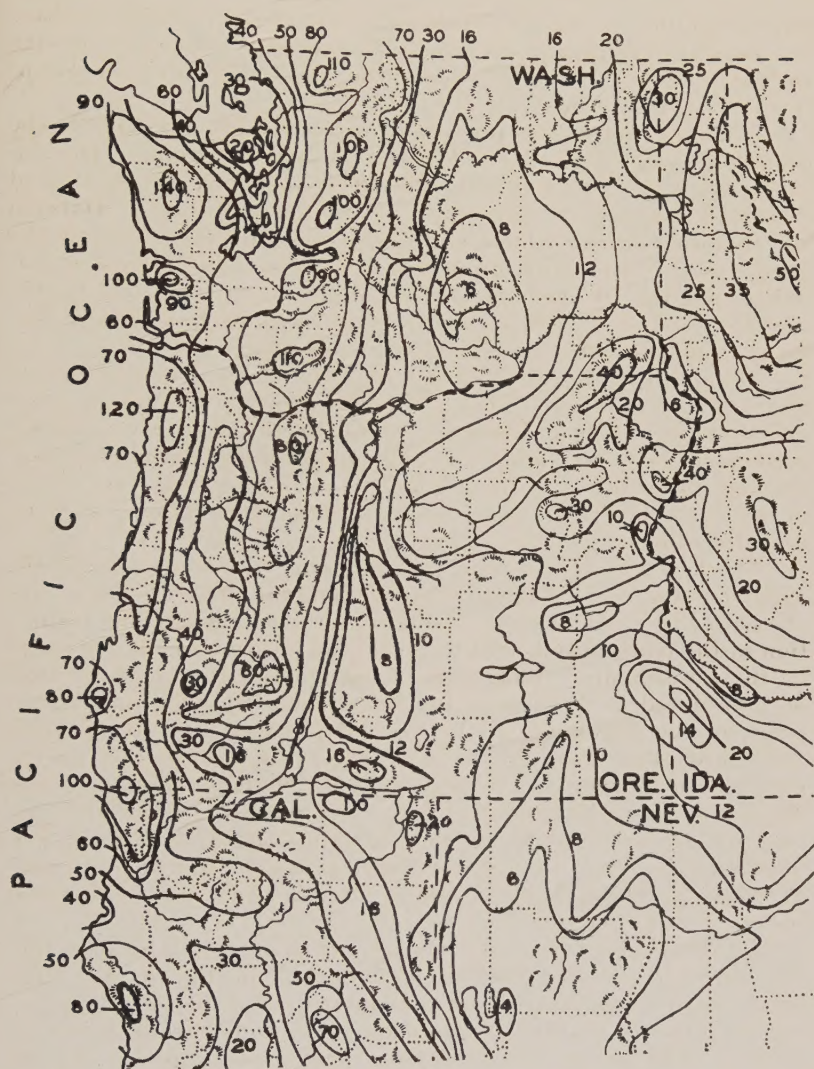


FIG. 1. Annual precipitation in inches in the Pacific Northwest.

the environmental centers of the vegetation areas for the region under consideration. The solid triangles in Figure 6 indicate the location of these centers.

Figure 6 shows, in addition to the environmental centers already mentioned, the limits of the floral areas of the Pacific Northwest. In fixing boundaries for the areas it was assumed that such boundaries should represent as nearly as possible for



FIG. 2. Average July temperature in °F. in the Pacific Northwest.

each climatic factor the isopleth marking the median point between gradient extremes. Since these isopleths do not coincide for all factors, it was necessary to establish a line which most nearly expressed their average. When so constructed, the boundaries between adjacent areas lie along the lines which are farthest removed from what might be termed the "influence" of their

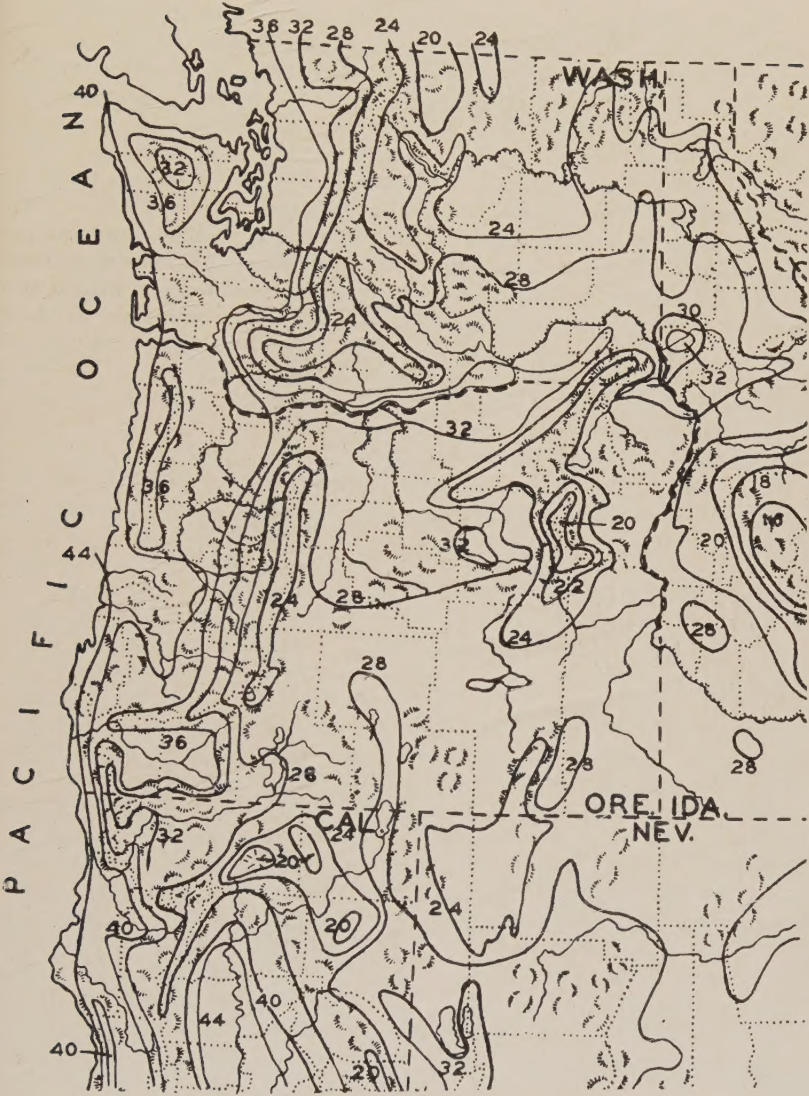


FIG. 3. Average January temperature in °F. in the Pacific Northwest.

respective centers of extremes. In other words, the territory within a vegetation area comprises what is environmentally most closely related to the point of greatest concentration of extremes around which the area is built. The sinuous courses frequently followed by the boundary lines correspond to the courses of some or all of the isopleths upon which they are based.

It should be emphasized that the important thing in each area is its center of environmental extremes, not its boundaries. This center is the center of endemism as well, and the farther we go from this point of greatest influence the less pronounced does endemism become, until at the boundary of the area the flora partakes equally of the characteristics of two adjacent floras.

It will be noted that in some instances more than one area is featured by the same combination of extremes. For example, most of the mountainous areas are characterized by high annual precipitation, low summer and winter temperatures and short growing season. It would seem that such similarity in climate would tend to cause a corresponding similarity in floras. Such areas, however, are always separated from one another by regions in which at least one, and sometimes more, of the climatic factors are at its opposite extreme. These intervening belts, because of this environmental difference, apparently serve as barriers to the migration and consequent mingling of many plant species.

The concept of vegetation areas based upon centers of environmental extremes offers an explanation for a number of features of the distribution of plant species in the Pacific Northwest. The location in western Nevada of the environmental center for the long arm that extends northward into southern Lake and Klamath counties in Oregon explains why so many species listed for the latter locality extend into California and Nevada rather than northward. Similarly, the location on the Columbia River of a center of an environmental unit including north central Oregon and central Washington explains why the flora of north central Oregon is so closely related to that of central Washington and so different from that of south central Oregon. The reason for the sharp break in the coastal flora in the vicinity of Coos Bay, Oregon, becomes evident when one notes the two coastal centers in Del Norte County, California, and near Grays Harbor, Washington. Another interesting question is, "Why is the Coast Range in Oregon a region with so few endemic species?" It will be noted on the climatic maps that there is no striking concentration of extremes in these mountains, a fact which probably accounts for the low degree of endemism. It is this lack of extremes which excludes the Coast Range as a vegetation area in the present scheme, although it has been so considered by other botanical writers.

THE VEGETATION AREAS OF THE PACIFIC NORTHWEST

The following summary of the vegetation areas attempts to present briefly the climatic features of each, along with the main floral elements which characterize the area. No attempt is made here to compile an extended list of endemic species, but merely to show the framework for each area, within which a greater or



FIG. 4. Average length in days of the growing season in the Pacific Northwest.

lesser number of endemics do occur, as may be ascertained by consulting any manual of the flora of the region.

The names selected for the areas are for the most part those of some geographical feature at or near the environmental center of the area.

The present treatment is limited to those areas occurring either wholly or in part in the states of Washington and Oregon, except

that the Sierra Area has been included because of its close floristic relationship with the areas of southern Oregon.

DEL NORTE AREA. This is a region of high annual precipitation, low summer temperatures, high winter temperatures and long growing season. The dominant species throughout much of the area is *Pseudotsuga taxifolia*, but the two most characteristic tree species are *Sequoia sempervirens* and *Chamaecyparis Lawsoniana*. Other species marking the area are *Umbellularia californica*, *Lithocarpus densiflora*, *Quercus chrysolepis*, *Ceanothus thyrsiflorus*, and *Rhododendron occidentale*.

NORTH COAST AREA. The climatic extremes here are the same ones found in the Del Norte Area, the most significant difference lying in the lower winter temperatures occurring in the more northerly area. *Pseudotsuga taxifolia* is again the dominant species, but *Sequoia sempervirens* and *Chamaecyparis Lawsoniana* are replaced by *Picea sitchensis* and notable stands of *Thuja plicata* and *Tsuga heterophylla*.

OLYMPIC AREA. This mountain massif, representing the highest elevation lying between the North Coast and Puget Areas, is the center of the extremes of high precipitation, low summer and winter temperatures, and short growing season. The dominant vegetation consists of a forest of *Pseudotsuga taxifolia*, *Thuja plicata* and *Tsuga heterophylla*. The occurrence of *Abies lasiocarpa*, *A. amabilis*, *A. procera*, *Tsuga Mertensiana* and *Chamaecyparis nootkatensis*, along with those species already named, emphasizes the general similarity of the flora of this area to that of the North Cascade. The Olympic Area, however, lacks the *Picea Engelmannii*, *Larix Lyallii* and *Pinus albicaulis* of the Cascades, as well as a number of herbaceous species as listed by Piper (1906). On the other hand, a considerable number of herbaceous or shrubby species are endemic to the Olympics.

SISKIYOU AREA. The mountain massif composed of the Siskiyou and Trinity mountains, marked by a high extreme of precipitation and low extremes of summer and winter temperatures and of growing season, is separated climatically from the similar extremes of the Cascade-Sierra divide by opposite extremes in the lower elevations of the Klamath, Pit and upper Sacramento valleys. The dominant vegetation in the western part of the area (its environmental center) is a *Pseudotsuga* forest mixed with *Lithocarpus densiflora* and *Quercus chrysolepis*. This changes eastward to a forest of *Pinus ponderosa* and *P. Jeffreyi*. The area is one of a high degree of floral endemism, marked by such species as *Pinus Balfouriana*, *Picea Breweriana*, *Cupressus MacNabiana*, *Juniperus californica siskiyouensis*, *Lithocarpus densiflora echinoides*, *Quercus Breweri*, *Q. Sadleriana* and *Q. vacciniifolia*.

ROGUE AREA. This area is one of relatively low rainfall, high summer temperature, moderate winter temperature, and long growing season. The dominant vegetation is a deciduous wood-

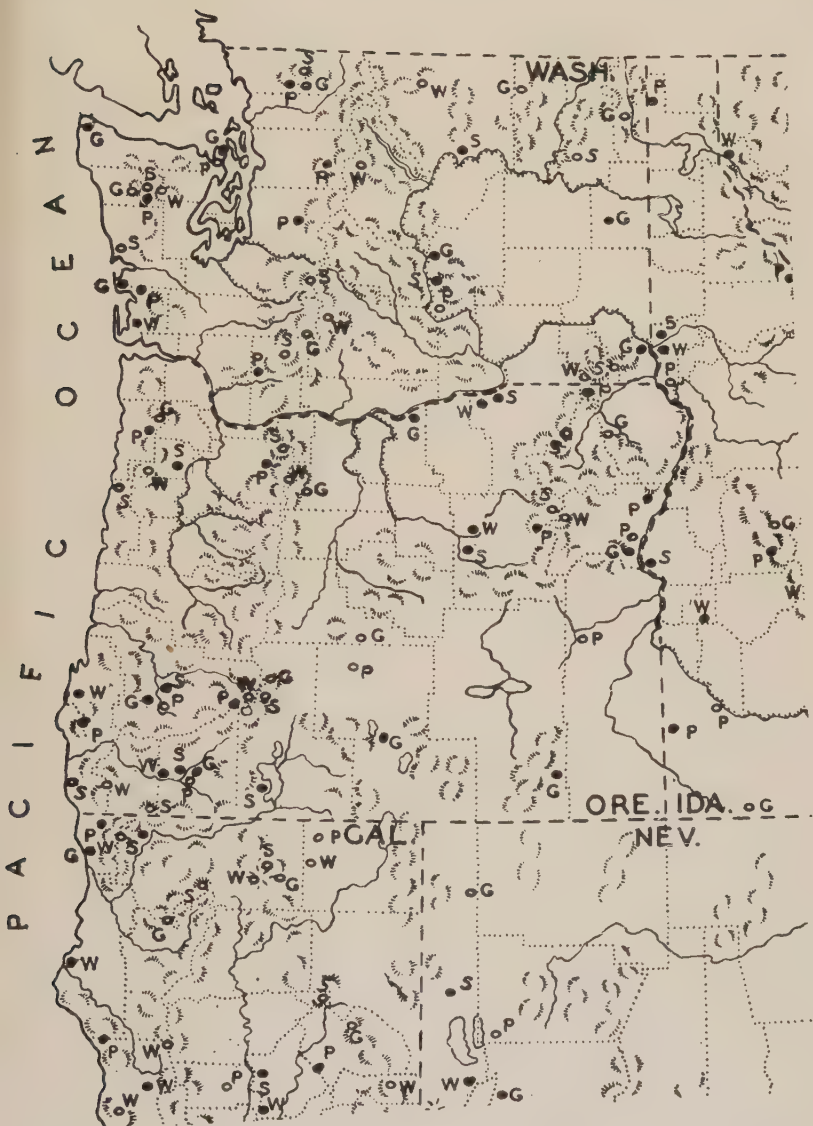


FIG. 5. Principal gradient extremes in the Pacific Northwest for annual precipitation (P), average July temperature (S), average January temperature (W), and length of growing season (G); high ●, low ○.

land consisting of *Quercus Garryana*, *Q. Kelloggii* and *Arbutus Menziesii*, with a generous mixture of *Pinus ponderosa*, especially on slopes just above the preceding. Important shrubs characterizing the area are *Rhus diversiloba*, *Ceanothus cuneatus* and *Arctostaphylos viscida*.

PUGET AREA. The great trough between the Coast Range and the Cascades, extending from Puget Sound southward to the Calapooya Mountains in Oregon, has the same climatic extremes as does the preceding area. However, at its center, on lower Puget Sound, the long growing season extreme is more pronounced than in the Rogue, the high summer temperature extreme is less pronounced, while winter temperatures are about the same. The vegetation of the Puget Area is predominantly the *Pseudotsuga* forest, mingled in cool valleys and on north slopes with *Thuja plicata* and *Tsuga heterophylla*, and in its drier phase with *Arbutus Menziesii* and *Quercus Garryana*. It lacks the *Picea sitchensis* of the adjacent North Coast Area, and the *Quercus Kelloggii* and *Pinus ponderosa* of the Rogue.

NORTH CASCADE AREA. The high mountains of this area result in a high extreme of precipitation, and low extremes in both winter and summer temperatures as well as in length of growing season. The vegetation at the altitudes where these extremes occur is a subalpine forest consisting of *Tsuga Mertensiana*, *Abies lasiocarpa* and *Pinus albicaulis*, flanked at lower elevations by *Pinus contorta Murrayana* and *Picea Engelmannii*, and by *Pseudotsuga taxifolia* mixed with *Abies procera* and *A. amabilis*.

SOUTH CASCADE AREA. This area, with climatic extremes similar to those of the preceding one, is separated from it physiographically and climatically by the break in the Cascade Range where the Columbia River cuts through. The plant species dominant in the North Cascade Area are present also in the South Cascade, but the association in the latter is altered by the addition of *Pinus Lambertiana*, *P. attenuata* and *Abies magnifica* and its variety *shastensis*.

SIERRA AREA. Geographically and physiographically this area occupies a position similar to that of the North Cascade and South Cascade Areas, and like them is marked by a high extreme of precipitation and low extremes of summer and winter temperature and of growing season. An environmental break at the Pit and Klamath rivers marks the transition from the flora of the South Cascade to that of the Sierra Area. Typical of the vegetation of the latter area are *Pinus Jeffreyi*, *P. Lambertiana*, *P. Sabiniana*, *Sequoia gigantea*, *Carpenteria californica*, *Jamesia americana californica*, *Staphylea Bolanderi*, *Rhamnus Purshiana anonaefolia*, *R. rubra*, *Ceanothus Lemmonii* and *Fremontia californica*.

COLUMBIA AREA. This comprises the valley of the middle portion of the Columbia River and the lower portions of its tributaries, chief of which are the Snake, Yakima, John Day and Deschutes.



FIG. 6. Vegetation areas of the Pacific Northwest. Triangles indicate the centers of environmental extremes.

Its low precipitation, high summer and relatively high winter temperatures and long growing season are extremes of climatic gradients whose opposite extremes are in the Cascade Mountains, Blue Mountains and Okanogan Highlands, which together roughly surround the area. The region is primarily grassland, with sage-

brush keenly competing with the grasses. Characteristic species are *Agropyron spicatum*, *Poa secunda* and *Artemisia tridentata*. In the more alkaline situations *Elymus glauca* and *Sarcobatus vermiculatus* are common. Along streams and in the canyons some of the species which mark the vegetation of this area are *Rhus glabra occidentalis*, *R. Toxicodendron* and *Prunus demissa*.

CLEARWATER AREA. Centered in the lower valley of the Clearwater River in Idaho, with its extremes of low rainfall, high summer and winter temperatures and long growing season, this area extends up the valleys of the Clearwater and its tributaries and out over the rolling hills of southeastern Washington. Its vegetation is typically a bunchgrass association like that of the Columbia Area to the west. The hills and lower mountains within its eastern limits support a forest of *Pinus contorta Murrayana*, *P. monticola*, *P. ponderosa* and *Pseudotsuga taxifolia*. No strictly endemic species appears to be sufficiently prominent to serve as a marker for the area, although a number of endemic species occur locally.

DESCHUTES AREA. This area, occupying the extreme northern portion of the Great Basin and the plateau region immediately adjacent to it presents, with a few local exceptions, a fairly uniform set of environmental conditions extending over a considerable territory. The climatic extremes featuring the area are low precipitation, low winter temperature and short growing season, but with no marked extreme of summer temperature. The vegetation is basically a desert shrub formation consisting of *Artemisia tridentata*, *Chrysothamnus* spp., and in the more alkaline localities *Sarcobatus vermiculatus*, *Grayia spinosa*, *Eurotia lanata*, *Kochia vestita* and various species of *Atriplex*. Arborescent species frequently occupying slopes and some of the higher elevations are *Juniperus occidentalis*, *Pinus ponderosa* and *P. contorta Murrayana*.

SNAKE RIVER AREA. The climatic center of this area, located along the Snake River in Washington County, Idaho, and Baker County, Oregon, differs from that of the adjacent Deschutes Area in its high winter and summer temperatures and long growing season. The general character of the vegetation, especially as it extends up the Snake River Valley across southern Idaho, is strikingly similar to that of the sagebrush plains of the Deschutes Area, and the species listed as characterizing the latter might be repeated for the region under discussion. However, especially in its northern extremity in the vicinity of its climatic center, endemic species or subspecies of more local distribution occur with sufficient frequency to emphasize the distinctiveness of its flora.

WASHOE AREA. The Washoe Area occupies that portion of the Great Basin lying just to the south of the Deschutes Area. Its climatic extremes, viz., low precipitation, high summer and winter temperatures and long growing season, are centered in the Pyra-

mid Lake Valley of western Nevada. The characteristic vegetation of this area is again desert shrub, and the species comprising this formation are largely the same as those in the Deschutes Area. However, the *Juniperus occidentalis* of the latter is here replaced by *J. utahensis* and *Pinus monophylla*, while other species distinguishing the Washoe Area include *Ephedra* spp., *Celtis Douglasii* and *Prunus Andersonii*.

BLUE MOUNTAIN AREA. The high precipitation, low summer and winter temperatures and short growing season of this elevated area represent the extremes of climatic gradients extending out into the valleys of the Columbia River to the northwest and the Snake River to the east and south. The lower levels of the climatic gradients are occupied by a forest of *Pinus ponderosa* associated with an undergrowth of *Ceanothus velutinus*. This forest is replaced toward the opposite extremes by *Pinus contorta Murrayana*, *Larix occidentalis*, *Abies grandis* and *Pseudotsuga taxifolia*. The Blue Mountain Area holds many species in common with the Rocky Mountains, but at the same time is characterized by the occurrence of many endemics.

OKANOGAN AREA. This comprises largely the mountainous region of northeastern Washington known as the Okanogan Highlands, with its extremes of high precipitation, low summer and winter temperatures and short growing season. The southern margin of the area, representing its lower environmental levels, is given over to a grassland formation similar in composition to the grasslands of the Columbia Area. Going toward the environmental center in the higher mountains the vegetation type changes progressively to forests of *Pinus ponderosa*, *Pseudotsuga taxifolia*, *Larix occidentalis*, *Pinus contorta Murrayana*, *Thuja plicata*, *Picea Engelmannii* and *Pinus monticola*. The area is also marked by the occurrence of *Juniperus scopulorum*, *Betula papyrifera occidentalis*, *Populus tremuloides aurea*, *Acer Douglasii*, *Ceanothus sanguineus*, *C. velutinus* and *Rhus glabra occidentalis*.

AREAL DISTRIBUTION IN A FEW PACIFIC NORTHWEST GENERA

That the areas delimited in the manner previously shown do constitute centers of endemism is indicated in the work of recent writers who have monographed plant genera or sections of genera which are well represented in the Pacific Northwest. An analysis of these monographs reveals that a relatively large number of species or subspecies are confined wholly or largely to a single area as here treated. A random selection from the monographs is presented in the following table, in which the first column indicates the number of species or subspecies occurring in the Pacific Northwest, and the second column the number of these which are endemic to one area. These endemics are then listed by name and their distribution indicated. Besides the species reported as

TABLE 1. AREAL DISTRIBUTION IN A FEW PACIFIC NORTHWEST GENERA

Total	Endemic		Del Norte	N. Coast	Olympic	Puget	Rogue	Siskiyou	N. Cascade	S. Cascade	Sierra	Columbia	Clearwater	Deschutes	Snake	Washoe	Blue Mts.	Okanogan
3	1	<i>Tofieldia glutinosa absoma</i>																x
11	7	<i>Camassia</i> <i>Quamash maxima</i> <i>Quamash azurea</i> <i>Howellii</i> <i>Quamash intermedia</i> <i>Quamash Walpolei</i> <i>Quamash utahensis</i> <i>Cusickii</i>			x	x		x	x	x					x			
15	6	<i>Erythronium</i> <i>Howellii</i> <i>oregonum leucandrum</i> <i>purpurascens</i> <i>tuolumnense</i> <i>multiscapoideum</i> <i>grandiflorum chrysandrum</i>					x				x				x			
24	14	<i>Calochortus uniflorus</i> <i>Howellii</i> <i>Greenei</i> <i>persistens</i> <i>monanthus</i>				x	x	x			x		x					

endemic to one area only, there are others which occur in two or three areas only, these areas being similar as to climatic extremes.

The genera and their monographers herein referred to are the following: *Tofieldia*, Hitchcock (1944); *Camassia*, Gould (1942); *Erythronium*, Applegate (1935); *Calochortus*, Ownbey (1940); *Arabis*, Rollins (1936); *Sedum*, Clausen (1942); *Penstemon*, Keck (1945); *Wyethia*, Weber (1946).

SUMMARY

In any region extensive enough to show physiographic variability, the climatic or other environmental factors occur as gradients. Previous investigation has shown that where several extremes of these gradients occur together they mark the center of an area rich in endemic plant species. In this study the Pacific Northwest has been divided into sixteen vegetation areas, each built around one of these centers of environmental extremes. Each area is briefly characterized as to its dominant plant association. Examples from the recent works of monographers show how the distribution of most plant species fits into the pattern of these areas.

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University of Oregon, Eugene

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THE GENUS *HELIANTHELLA* IN OREGON

WILLIAM A. WEBER

Dr. Morton E. Peck's Manual of the Higher Plants of Oregon (1941) listed *Helianthella Douglasii* T. & G. as the sole species then known to occur in that state. The present paper brings to the attention of students of the Oregon flora three previously unreported species in this genus of Compositae and presents a simple key to all the species now recorded from Oregon.

The collections upon which these new records are based are not recent ones; on the contrary, they were made about fifty years ago and are probably widely distributed in herbaria, but for want of critical examination these have passed for individuals of the common *H. Douglasii*.

An annotated list of the Oregon species of *Helianthella* follows. All specimens cited are from the herbarium of the United States National Museum.

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HELIANTHELLA QUINQUENERVIS (Hook.) A. Gray in Proc. Amer. Acad. 19: 10. 1883. *Helianthus quinquenervis* Hook. in Lond. Jour. Bot. 6: 247. 1847. Warner Range, Lake County, Oregon, 1650 m. alt., July 26, 1896, *F. V. Coville* & *J. B. Leiber* 52. The westernmost station previously recorded for this essentially Rocky Mountain species was in Elko County, Nevada.

HELIANTHELLA UNIFLORA (Nutt.) T. & G., Fl. N. Am. 2: 334. 1842. *Helianthus uniflorus* Nutt. in Jour. Acad. Sci. Phila. 7: 37. 1834. White Horse Mts., south of old Fort Smith, Harney County, southeastern Oregon, Aug., 1901, *David Griffiths* & *E. L. Morris* 450.

HELIANTHELLA UNIFLORA (Nutt.) T. & G. var. *Douglasii* (T. & G.) comb. nov. *Helianthella Douglasii* T. & G., Fl. N. Am. 2: 334. 1842. The common *Helianthella* in central and northeastern Oregon from the Ochoco Mountains to the Wallowa Mountains and northward into Washington, northern Idaho, Montana, and British Columbia appears to be a weakly differentiated northward extension of *H. uniflora* of the Rocky Mountains and Great Basin ranges. Its larger flower heads, ciliate rather than uniformly cinereous-pubescent phyllaries, and its occurrence at lower altitudes separate the present race from *H. uniflora* proper. Although most specimens may be placed without much difficulty

in either of these two racial categories, transitional intermediates do occur.

KEY TO THE OREGON SPECIES OF HELIANTHELLA

- Cauline leaves alternate, except the lowermost pair. Leaves chiefly basal, at the summit of a slender caudex..... *H. californica*
var. *nevadensis*
- Cauline leaves opposite. Leaves chiefly cauline. Caudex stout.
- Cauline leaves attenuate at both ends, long petiolate. Phyllaries ovate, conspicuously ciliate, blackish on drying *H. quinquenervis*
- Cauline leaves merely acute, short-petiolate or sessile. Phyllaries lanceolate, variously pubescent, drying green.
- Heads large, 2.0-2.5 cm. broad excluding the rays. Phyllaries ciliate..... *H. uniflora*
var. *Douglasii*
- Heads small, 1.5-2.0 cm. broad excluding the rays. Phyllaries uniformly cinereous-pubescent..... *H. uniflora*

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A NEW POLEMONIUM FROM MEXICO

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Polemonium glabrum sp. nov. Erecta, humilis, 2-3 dm. alta; rachis foliis angustate-alatis; foliolis 6-8-junctis, glabris vel ciliatis; calycis glabris, angustate-campanulatis, 10 mm. longis, segmentis angustatis acutis, tubis æqualibus; corollis cæruleis, infundibuliformibus, 25-30 mm. longis, 15-20 mm. latis, lobis tubarum brevioribus, spathulatis, apiculatis.

A slender erect perennial 2-3 dm. tall from a rootstock or horizontal rhizome; leaves 4-8 cm. long with 13-17 leaflets 3-11 mm. long, 2-4 mm. wide, elliptical, acute, glabrous or ciliate on a slightly winged rachis, the bases of the distal five leaflets commonly confluent; calyx glabrous, narrowly campanulate. 10 mm. long, 4 mm. broad, the segments narrow, acute, equalling the tube; corolla blue, truly funnellform in limb as well as in tube, 25-30 mm. long, 15-20 mm. broad, the lobes two-thirds as long as the tube, spatulate and apiculate; stamens inserted 3 mm. from the base of the corolla-tube, pubescent at, and slightly above, the point of insertion, 20 mm. long; style slightly exceeding the stamens, shorter than the corolla; capsule ovoid, many seeded; seeds not becoming mucilaginous when wet.

Type. Mt. Mohinora (10 miles west of Guadalupe y Calvo), southwest Chihuahua, Mexico, September 1, 1898, *E. W. Nelson* 4865 (United States National Herbarium).



PLATE 23. *POLEMONIUM GLABRUM*. Fig. 1, habit, $\times \frac{1}{2}$. Fig. 2, calyx, $\times 1\frac{1}{2}$. Fig. 3, floral dissection, natural size. Fig. 4, capsule dissection, $\times 1\frac{1}{2}$. Fig. 5, leaf apex, $\times 1\frac{1}{2}$.

Polemonium glabrum may be distinguished readily from any other naturally occurring *Polemonium* by the shape and size of the corolla, and by its glabrous calyx. The only other record of a similar corolla is found in the report by Ostenfeld (Genetic studies in *Polemonium*, Hereditas 12: 31-39. 1929.) of crosses between *P. mexicanum* Cerv. ex Lag. and *P. pauciflorum* S. Wats. The affinities of the present species may well be with the above, but neither *P. mexicanum* nor *P. pauciflorum* have been reported from the vicinity of *P. glabrum*. The probability of *P. glabrum* being merely a hybrid (*P. mexicanum* × *pauciflorum*) was considered and discounted because of the absence of the putative parents and because of its constant pollen size. The pollen of known hybrids has been found by the author to show irregularities in size, whereas the pollen of *P. glabrum* is perfectly normal. Also there is apparently no reduction in the number of seeds set, as might be expected in the case of a hybrid plant.

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NOTES ON THE TAXONOMY OF SOME EASTERN ASIATIC FERNS OF THE GENERA PROTO- WOODSIA AND PTERETIS

CLYDE F. REED

While glancing over a recent paper of Dr. R. C. Ching (1945, p. 36) and a review of the same paper in Biological Abstracts (1946), the author noticed the generic name *Proto-woodsia* being used for a new genus of ferns. Since he was familiar with this name as early as 1941, verifying the validity of the name seemed necessary. In checking over his notes, the author found the following sequence of circumstances.

In 1940 Dr. Ching (p. 245) used the generic name *Proto-woodsia*, listing under it "*P. manchuriensis* (Hook.) Ching. A monotypic genus confined to N. E. Asia." The only description of the genus is to be found in his description of the new family Woodsiaceae, as "spores bilateral, dark-colored, with perispores, or tetraedral, smooth and translucent (*Protowoodsia*)." Concluding his description of the Woodsiaceae, Ching remarks that this is "a very small family of two genera and about forty species; its affinities with *Cyathea* and the next two families has generally been recognized."

The manner in which the name *Protowoodsia* appeared in Ching's paper led the author to believe that the generic name had been validly published elsewhere. Therefore, in his doctorate thesis in 1942 (p. 73), the author used the generic name as follows: "*Protowoodsia* Ching has translucent, smooth, subglobose to bilateral spores lacking an exospore (*P. manchuriensis*).

sis)." After studying the spores of specimens of *Woodsia manchuriensis* from Japan and Korea (from herbarium sheets at the Gray Herbarium), I am unable to verify the "tetraedral" spores Ching had described *Protowoodsia* as possessing.

In 1945 Ching (p. 36) published the genus *Protowoodsia* properly, accompanied with a Latin description and with citations of the specific transfers. The following is Dr. Ching's description as originally written:

"*PROTOWOODSIA*, gen. nov. Genus *Woodsiae* § *Euwoodsia*, habitu, configuratione et stipite continuo similis, differt praecipue folia utraque nuda, pilis articulatis et paleis brunneis linearibus desunt, indusiis inferioribus globosis griseo-membranaceis, satis magnis, apice ore rotundata contracto dehiscentibus, spores tetraedricae, translucetibus, laevibus.

Species unica in Asia boreali-orientalis incola."

Again, Dr. Ching describes the spores as being "tetraedral" in shape. However, the apparently invalid use of the combination *Protowoodsia manchuriensis* (Hook.) Ching, as well as of the generic name, in the Sunyatsenia publication are totally ignored in the later publication. Obviously, the earlier publication was a prepublication.

The spores in the specimens studied by the author are subglobose, totally lacking any trace of the triradiating crest so prevalent in tetrahedral spores. They are definitely monolete, subglobose to ellipsoidal in shape and light brown in color, lacking an exospore, and therefore appearing smooth. Dr. Ching called the loose outer covering of the spores the perispore; I have designated it as the exospore. The perispore, which is the outer spore-wall, in the case of *Woodsia manchuriensis* has a few broad pits, but is otherwise smooth.

While studying the annular cells of the sporangia of various species of the genus *Woodsia*, I observed that the range of variability in the number of cells in the annulus is confined to groups of species. In Table 1 are given some of the species studied, the locality of the specimens, and the number of cells in the annuli.

Judging from the range in the number of cells in the annulus in *P. manchuriensis* (10-13), it belongs by itself. The spores and the indusium also bear out isolating this species, probably in the new genus *Protowoodsia*, as proposed by Ching, with an emendation in regard to the spore characters.

PROTOWOODSIA Ching, Sunyatsenia 5(4): 245 (nomen subnud.). 1940; Lingnan Sci. Jour. 21: 36. 1945.

PROTOWOODSIA MANCHURIENSIS (Hook.) Ching, Sunyatsenia 5(4): 245 (nomen subnud.). 1940; Reed, Thesis, Harvard Univ., p. 73. 1942 (ined.); Ching, Lingnan Sci. Jour. 21: 36. 1945.
Syn.: *Woodsia* (*Physematium*) *manchuriensis* Hook., 2nd. Cent.

Ferns, pl. 98. 1861; *Diacalpe manchuriensis* Trev., Nuov. Giorn. Bot. Ital. 7: 160. 1875; *Physematium manchuriense* Nakai, Bot. Mag. Tokyo 39: 176. 1925; *Woodsia insularis* Hance, Ann. Sci. Nat. IV. 15: 228. 1861 (non sensu Baker, in Hook., Syn. Fil. ed. 2, 47. 1874).

Distribution: North China, Korea and northern part of Japan.

Another case of "prepublication" in these papers of Dr. Ching (1940, p. 224) is the combination *Pteretis intermedia* in the de-

TABLE 1. SUMMARY OF THE CELL NUMBER IN THE ANNULUS.

Species	Locality	Number of cells in annulus
<i>Woodsia lanosa</i>	Kansu	26, 27, 28, 27, 27, 26, 28.
<i>W. glabella</i>	Newfoundland	23, 25, 26, 23, 21, 22, 25, 21.
<i>W. glabella</i>	Spitzbergen	19, 17, 19, 21, 17.
<i>W. macrospora</i>	Kansu	24, 23, 22, 23, 23, 23.
<i>W. elongata</i>	Kumaon	21, 24, 23.
<i>W. oregana</i>	Quebec	24, 18, 18, 20, 20, 23, 17, 18, 21.
<i>W. cathcartiana</i>	Michigan	20, 21, 23, 21, 18, 17, 18, 23.
<i>W. ilvensis</i>	Newfoundland	20, 21, 26, 20, 21, 21, 22, 21.
<i>W. alpina</i>	New Brunswick	20, 18, 15, 18, 16, 17.
<i>W. fragilis</i>	Caucasus	18, 18, 20, 18, 19, 18, 18.
<i>W. polystichoides</i>	Manchuria	20, 17, 19, 18, 19, 17, 18.
<i>W. subcordata</i>	Manchuria	17, 17, 17, 17, 17.
<i>W. peruviana</i>	Peru	18, 17, 18, 18, 18.
<i>W. crenata</i>	Bolivia	18, 18, 16, 17, 17, 16.
<i>W. montevidensis</i>	Brazil	17, 16, 17, 17.
<i>W. mexicana</i>	New Mexico	15, 17, 16, 17, 16, 18, 17, 18.
<i>W. Plummerae</i>	Arizona	14, 15, 14, 15, 16, 15.
<i>W. mollis</i>	Mexico	15, 14, 14.
<i>W. scopulina</i>	South Dakota	15, 15, 16, 16, 15, 16.
<i>W. obtusa</i>	Maryland	14, 14, 15, 15, 14, 14, 17, 16.
<i>Protowoodsia manchuriensis</i>	Japan & Korea	12, 12, 10, 12, 10, 12, 13, 12.

scription of the new family Onocleaceae. In describing the family there appears the following passage: "... sori superficial. dorsal on the veins, globose, borne on cylindrical or convex receptacle and provided with white, membranaceous, fugaceous inferior, shell-shaped or globose indusium (lacking in *Pt. intermedia*). . . ." Ching only recognized two genera in the family, saying nothing of the genus *Pentarhizidium* of Hayata (1927, p. 716 and 1928, p. 345). However, at this place Ching does not cite the author of the specific epithet *intermedia*.

In his thesis again the present author (1942, p. 70) recognized three genera as follows, based on spore characters: "In *Onoclea* L. there are from thirty to thirty-two cells in the annulus. The spores (*O. sensibilis*) are green, large, bilateral, with a large loose punctate exospore. In *Pentarhizidium* Hayata the spores are similarly green, large, bilateral, with a very large loose punctate exospore (*P. orientale*). The annulus has from thirty-three to thirty-four cells.

In *Pteretis* Raf. (*Matteuccia* Todaro) the spores are brownish, with a smooth exospore, about one-half the size of those in *Onoclea* and *Pentarhizidium* and of entirely different structure. There are only twenty to twenty-seven cells in the annulus."

In 1945 Dr. Ching (p. 36) makes the new combinations *Pteretis japonica* (Hay.), *Pteretis intermedia* (C. Chr.) and *Pteretis orientalis* (Hook.), citing the proper synonyms for the specific epithets. Ching has taken the three species Hayata had placed in *Pentarhizidium* and transferred them to *Pteretis*, thus reducing the former genus to *Pteretis*.

The sori in *Pteretis* are medial and biserial, protected by a marginal lobe; in *Pentarhizidium* the sori are intramarginal and uniserial, protected by the continuous dark-brown leaf-margin. The spores of these two genera differ as stated above. The number of cells in the annulus is quite significant: *Pentarhizidium* having thirty-three to thirty-four cells with four to seven stomium-cells besides; *Pteretis* having twenty to twenty-seven rarely thirty, cells with four to six stomium-cells. These are probably distinct genera.

PTERETIS Raf., Amer. Monthly Mag. Crit. Rev. 2: 268. 1818; Nieuwland, Amer. Midl. Nat. 3: 197. 1914; 4: 334. 1915; C. Chr., Ind. Fil. Suppl. 2: 30. 1917; Small, Ferns Vicinity of New York, 140-143, fig. 1935; Mattfeld, Repert. Sp. Nov. Fedde 44: 289. 1938; Merrill, Amer. Fern Jour. 33: 55-56. 1943.

Syn.: *Onoclea* Hoffm., Deutsch. Fl. 2: 11. 1795 (*partim*); Michx., Fl. Bor. Amer. 2: 272. 1803; Hook., Sp. Fil. 4: 161. 1862; Hook. et Bak., Syn. Fil. 46. 1866; *Struthiopteris* Willd., Mag. Ges. Nat. Fr. Berlin 3: 160. 1809 (*non Struthiopteris* Weis, 1770 *nec Struthiopteris* Bernh., 1801); *Pterilis* Raf., Amer. Monthly Mag. Crit. Rev. 4: 195. 1819; *Pterinodes* Kuntze, Rev. Gen. Pl. 2: 819. 1891 (*partim*); *Matteuccia* Todaro, Syn. Pl. Acot. Vasc. Sicilia, 30. 1866.

This genus contains the European species *Pteretis Struthiopteris* (L.) Nieuwl. (Amer. Midl. Nat. 3: 197. 1914) and the American species *Pteretis nodulosa* (Michx.) Nieuwl. [Amer. Midl. Nat. 4: 334. 1916 (1915)].

PENTARHIZIDIUM Hayata, Bot. Mag. Tokyo 41: 715-716. 1927; 42: 345. 1928.

PENTARHIZIDIUM INTERMEDIUM (C. Chr.) Hayata, Bot. Mag. Tokyo 41: 715. 1927; 42: 346. 1928.

Syn.: *Matteuccia intermedia* C. Chr., Bot. Gaz. 56: 337. 1913; *Pteretis intermedia* (C. Chr.) Ching, Sunyatsenia 5(4): 224 (nomen nudum). 1940; Reed, Thesis, Harvard Univ., p. 70. 1942 (ined.); Ching, Lingnan Sci. Jour. 21: 36. 1945.

Distribution: China (Shensi and N.W. Yunnan), India (Sikkim).

PENTARHIZIDIUM JAPONICUM Hayata, Bot. Mag. Tokyo 42: 345. 1928.

Syn.: *Matteuccia japonica* (Hayata) C. Chr., Ind. Fil. Suppl. 3:

127. 1934; *Pteretis japonica* (Hayata) Ching, Lingnan Sci. Jour. 21: 36. 1945.

Distribution: Japan.

PENTARHIZIDIUM ORIENTALE (Hook.) Hayata, Bot. Mag. Tokyo 41: 715-716. 1927; 42: 345. 1928.

Syn.: *Struthiopteris orientalis* Hook., 2nd. Cent. Ferns, pl. 4. 1860; *Onoclea orientalis* Hook., Sp. Fil. 4: 161. 1862; Syn. Fil. 46. 1867; *Matteuccia orientalis* (Hook.) Trev., Atti Ist. Veneto III. 18: 586. 1869; C. Chr., Ind. Fil. 420. 1906; *Pteretis orientalis* (Hook.) Ching, Lingnan Sci. Jour. 21: 36. 1945.

Distribution: Temperate China, East Himalayas and Japan.

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REVIEW

A study of the genus Paeonia. By F. C. STERN. London, Royal Horticultural Society. viii + 155 pp., 15 colored plates, 28 text figures, 8 maps. 1946. 63s.

There is probably no group of non-professional botanists to whom plant science owes a greater debt than the botanical and horticultural enthusiasts of Great Britain. Their energy in gathering together collections of both specimens and living plants from all corners of the earth, their care in raising a great variety of rare, exotic, and "difficult" species in their gardens, and their generosity in financing the explorations and research studies of their friends in the professional field of botany has widened immensely our knowledge of the world's flora. And their standards of execution have been consistently high, both as to the accuracy of the research and the elegance of the publication. Consequently it is more of a pleasure than a surprise to learn that during Britain's "darkest hour" of the last war there was being prepared a botanical work which is not only a fitting successor to

its great array of predecessors, but which in addition is in many ways a model for progressive monographic studies of the future.

Mr. F. C. Stern's work on *Paeonia*, modestly entitled a "study," is actually a magnificent folio volume, superbly illustrated with accurate and highly artistic color plates of most of the species, supplemented by line drawings of some of the technical details and a complete set of distributional maps. The technical portions of the monographic treatment; nomenclatural history, synonymy, species descriptions, and discussions of diagnostic morphological characters, are full and accurate. The artificial key to the species is concise and as easy to follow as one can make it in a genus like *Paeonia*, which simply does not have the clear cut diagnostic characters found in many other groups. Most of the species descriptions are accompanied by helpful and well written accounts of the appearance of the living plants and of the proper methods of culture. Mr. Stern has shown that he is not an amateur in any sense of the word which refers to his degree of competence, but that in regard to its literal meaning he is a true lover of the plants to which he has devoted so much of his life.

But even more interesting than these parts of the work are the sections on the cytology and distribution of the species. The chromosome numbers are given of 34 of the 47 species, varieties, and forms; of the 13 not listed, 8 are poorly differentiated varieties of species of which the number is known, 2 are members of the tetraploid *mascula* and *officinalis* complexes, and undoubtedly have the same numbers as their close relatives; and the remaining three are the rare *P. kesrouanensis*, native to Syria, and two closely related endemics of southwestern China, *P. Mairei* and *P. oxypetala*. *Paeonia* thus ranks with *Crepis*, *Nicotiana*, and *Gossypium* as one of the best known cytologically of plant genera. The species are all either diploids with the somatic number $2n = 10$, or tetraploids with $2n = 20$.

The patterns of distribution of the various species provide material for a most interesting discussion. Endemism is common in the genus; 8 of the 33 recognized species are restricted to a single island, mountain range, or other small area. The genus as a whole occurs in five disjunct areas; the Mediterranean region; central Asia from the Urals to Siberia with an outlier in eastern Lapland; the western Himalaya; eastern Asia from southwestern China to Manchuria and Japan; and Pacific North America. Such a distribution is evidence of the great age of the genus, as is also the primitive nature of its morphological characteristics. Stern points out that the cytological condition of the species is characteristic for each separate area of distribution. North America contains only two diploid species, which have a distinctive type of chromosome behavior at meiosis. The species of eastern Asia are diploid with one exception, while those of Central Asia and the Himalaya are strictly diploid. The Mediterranean species

include both diploids and tetraploids, with the latter having by far the widest distributions. This latter fact brings forth a very plausible hypothesis as to the origin of these tetraploids. The diploid species are believed to be preglacial relics, which were pushed southward by the advancing ice sheet of the Pleistocene period, and took refuge in the islands of the Mediterranean and other warm areas. The tetraploids, which are believed to have arisen from the diploids by autopolyploidy, were supposedly the only forms which were able to migrate northwards in postglacial times.

There are probably few genera about which two botanists, studying the species independently and with different materials available, would agree completely as to the true relationships and boundaries of the species. *Paeonia* is no exception. The writer has spent some time studying this genus, his work being based largely on the living plants and interspecific hybrids kindly made available to him by Dr. A. P. Saunders of Clinton, New York, but supplemented by inspection of nearly all of the specimens available in American herbaria. His synopsis (Univ. Calif. Publ. Bot. 19: 245-266. 1939) differs in some respects from the arrangement of the species as given by Stern, and the evidence presented in Mr. Stern's study has not been sufficient to persuade him to change more than a few of his concepts, except in the case of names which must be altered for nomenclatural reasons.

In the first place, Mr. Stern's concept of the species is entirely morphological, and based chiefly on the ease with which they can be recognized in herbarium specimens. The present writer concluded that the three sets of characters which most sharply set off the majority of the species are those of the sepals, the carpels and stigmas at anthesis, and the mature seeds. Since, as Mr. Stern states, none of these can be readily studied in herbarium specimens, they are not included in either his key or the species descriptions. In the writer's decisions as to which forms should be recognized as species and which as subspecies, the ability of forms to cross in the garden and form fertile hybrids played an important role, particularly if the types concerned were known to occur naturally in the same or adjacent regions. Mr. Stern refers in some instances to the observation of the writer and Dr. Saunders that certain types hybridize freely in the garden, but fails to mention the significant fact that in those instances where the genetic evidence caused the writer to group different forms into the same species, as in *P. Delavayi*, *P. lutea*, and *P. Potanini*; and in *P. daurica* ("*P. triternata*") and *P. Mlokosewitschii*; the hybrids formed were fully fertile. Some valid species, like *P. Veitchi* and *P. Emodi*, as well as *P. daurica* and *P. tenuifolia*, also hybridize easily, but produce almost completely sterile F_1 hybrids characterized by very irregular meiosis. On the other hand Mr. Stern places in the same species as the yellow flowered *P. Wittmaniana* the plant from

the Caucasus first believed by Dr. Saunders and the writer to be *P. macrophylla* and later *P. tomentosa*. This plant has white, not yellow flowers; its sepals and petals are much broader than those of *P. Wittmaniana*, and the shape of the sepals is entirely different; its carpels are not only tomentose, but both the shape of the carpels and that of the stigmas is entirely different from those of the yellow flowered form recognized by Stern as *P. Wittmaniana* var. *nudicarpa*. Furthermore, the hybrid between these two forms is completely sterile. In every respect they appear to the writer far more distinct than such species as *P. arietina* and *P. officinalis*, which Stern places in different subsections of the genus, but which are able to form fully fertile hybrids.

Considerations like these cast considerable doubt on the validity of the two subsections recognized by Stern in the section (or subgenus) *Paeon*, namely *Foliolatae* and *Dissectifoliae*. They are in general distinct and natural groupings, but exceptions to this situation exist in the species groups of *P. officinalis*, *P. peregrina*, and *P. arietina*, all of them tetraploid, and admittedly by far the most difficult species groups in the genus. Mr. Stern has done a great service in describing the characteristics of leaf morphology by which their "species" may be identified, and in stating clearly their geographic distributions. But his evidence that they occur in adjacent areas rather than together in the same region, and that in at least some instances they intergrade where their ranges overlap, suggests to the present writer that they represent members of a typical "Rassenkreis" or polytypic species as recognized by zoologists, and that each of Mr. Stern's "species," in these three groups, with the exception of the more distinct and cytologically diploid *P. Clusii*, is a typical geographic subspecies. This point of view is supported by the hybridization experiments of Dr. Saunders.

That these differences of opinion in regard to the limits of species are not purely academic is evidenced by the fact that Mr. Stern and the writer hold opposite points of view in regard to the nature and origin of the tetraploids. His hypothesis that they arose and spread in response to the climatic changes which took place during the Pleistocene epoch is entirely plausible, but the belief that each tetraploid species arose separately and independently as an autotetraploid from a different diploid species is not in accord with a number of facts. In the first place, many of the tetraploids could, on morphological grounds, be just as easily connected with an entirely different diploid species from the one chosen by Mr. Stern. For instance, a comparison of the illustrations in Mr. Stern's study suggests that *P. Russi*, which he relates to *P. Cambessedesii*, is in many respects like *P. Broteri*, and could be derived from that species almost as easily, and study of details of floral structure supports this view. *P. mascula*, which is considered to be derived from *P. daurica*, is in many respects equally

similar to *P. Cambessedesii* and *P. Broteri*, and Stern remarks (p. 68) that "the form of *P. mascula* in Sicily looks very like *P. Russi* when examined as dried specimens." *P. banatica*, which such botanists as Kitaibel, and Ascherson and Graebner have considered to be a variety of *P. officinalis*, is regarded by Mr. Stern as derived from *P. mascula*, and so indirectly by autotetraploidy from *P. daurica*. But in the descriptive section he states (p. 72): "It is difficult to say whether this plant may be a variety of *P. mascula* or of *P. arietina*, since it has some of the characters of both of these paeonies." *P. arietina* is believed to be an autopolyploid from *P. rhodia*, a species very different from *P. daurica*. Finally, Mr. Stern considers that the two genetically isolated species grouped by him under *P. Wittmaniana* are autopolyploids of *P. Mlokosewitschii*. But although *P. daurica* and *P. Mlokosewitschii* are interfertile and differ in nothing except flower color and leaf shape, their two supposed autotetraploids, *P. mascula* and *P. Wittmaniana* (including *P. tomentosa*) are widely divergent in a number of morphological characteristics, and would almost certainly form highly sterile hybrids if intercrossed.

All of these facts support the writer's belief that the tetraploid peonies of the Mediterranean region form a typical polyploid complex, in which autopolyploidy has figured to a certain extent, but of which the majority of the species are allopolyploids derived from crossing between either the present day diploids or their ancestors or autopolyploid forms. Those belonging to the subsection *Foliolatae* are derived from the diploids of this subsection, *P. Cambessedesii*, *P. Broteri*, *P. rhodia*, and *P. daurica*. But the tetraploid *Dissectifoliae*, namely *P. officinalis* and its relatives, probably represent ancient allopolyploids involving on the one hand Mediterranean diploids, like *P. Clusii*, *P. rhodia*, and *P. daurica*, and on the other, the central Asiatic *P. anomala*. The best morphological evidence for this hypothesis lies in the appearance of *P. peregrina*, the most easterly of these tetraploids, which is one of the two species for which Mr. Stern could not find a diploid ancestor. But *P. officinalis*, which Mr. Stern believes to be an autotetraploid of *P. Clusii*, differs from the latter species in its relatively narrow leaves, while the most common effect of autopolyploidy on leaf shape in dicotyledons is to make the leaves shorter and broader. The influence of *P. anomala*, which has narrow as well as strongly lobed leaflets, would tend to produce precisely the divergence in leaf shape which is found in *P. officinalis* and *P. peregrina* as compared to *P. Clusii*. Furthermore, these tetraploids have one leaf characteristic not observed by Mr. Stern which is characteristic of *P. anomala* and its relatives, but is not found in any of the Mediterranean diploids, including *P. Clusii*; namely the presence of short, scabrous pubescence along the veins of the upper surface of the leaf. Finally, the hybrids produced by Dr. Saunders between *P. Mlokosewitschii* and *P. anomala* as well as *P.*

Veitchii resemble closely members of the *P. officinalis* complex in all of their features of external morphology.

The cytological evidence, also, supports the present writer's hypothesis. In the species of *Paeonia*, with their large chromosomes and random distribution of chiasmata, a high proportion of multivalents is to be expected if the component genomes of a tetraploid are completely homologous, or even if they are not quite so. But in most of the tetraploids investigated by the writer and Mr. S. O. S. Dark (Jour. Genetics 32: 353-372) including *P. officinalis*, *P. peregrina*, and *P. Wittmaniana*, the number of quadrivalent configurations per nucleus is only one or two, with most of the chromosomes paired as bivalents. This would suggest that the four component genomes of these tetraploids are not completely homologous, and that they belong to the category recently characterized by the writer (Advances in Genetics 1: pp. 417-421) as segmental allopolyploids, or polyploids of which the component genomes bear the majority of their chromosomal segments in common, but in which these genomes differ from each other by a large enough number of such segments so that free interchange between them is barred by complete sterility on the diploid level. The fact that most diploid inter-specific hybrids of *Paeonia* may form as many as four or five bivalents suggests that polyploids derived from them would be of this nature.

The hypothesis that the members of the *P. officinalis* complex arose as allotetraploids from hybrids between the Mediterranean diploids and *P. anomala* presupposes that at the time when these hybridizations took place the distributions of the diploid species were very different from what they are now. But both Mr. Stern and the writer are agreed that the present Mediterranean diploids are relics which had a considerably wider distribution before the beginning of the Pleistocene ice age. And fossil remains of late Tertiary age from western Europe, particularly the abundant seeds collected by Reid and Reid in the Pliocene deposits of the lower Rhine basin, contain a large proportion of species of flowering plants now confined to Asia, indicating the presence of a strong Asiatic element in the European flora at that time, which might easily have included *Paeonia anomala* or a relative of that species. The writer, therefore, would like to modify Mr. Stern's hypothesis in regard to the origin and evolution of the tetraploid species of *Paeonia*, and believes that they originated through a series of hybridizations between diploid species or their auto-tetraploid derivatives. The first of these hybridizations took place not later than the middle or end of the Pliocene epoch, but the process very likely was continued during the interglacial periods of the Pleistocene. The tetraploids have persisted and spread not only because of such beneficial qualities as might have been given them by their increased chromosome number, but also, and perhaps chiefly because they possess favorable combinations

of genes derived from ecologically as well as morphologically different ancestral species, which gives them a relatively wide range of tolerance of diverse ecological conditions.

The final decision as to the correctness of one or the other of these hypotheses, as well as to the validity of the writer's species concepts insofar as they differ from those of Mr. Stern, cannot be made through any attempt to improve on Mr. Stern's fine monographic study by means of examining further the herbarium specimens and garden plants now available to us. Careful studies are needed of the critical species as they grow in nature, and the splendid series of interspecific hybrids produced by Dr. A. P. Saunders needs to be increased and studied more carefully. Unfortunately the present state of the world makes both of these types of studies seem like remote ideals rather than actualities for the immediate future. Such parts of the globe as Dalmatia, Greece, Syria, and the Caucasus are considered by most people at present to be critical areas for very different reasons from the fact that those regions will yield important information about the relationship of *Paonia* species. And the years of labor and devotion expended by Dr. Saunders on his beautiful creations are a scarce commodity in this age of fear, hurry, and utilitarianism. But peonies have existed on this earth for many millions of years, and they will still be with us when the world settles down to a more normal way of living. And when that time comes, Mr. Stern's "study" may be looked upon as one of the outstanding achievements of the present period in the history of plant science.—G. L. STEBBINS, JR., University of California, Berkeley, California.

NOTES AND NEWS

RANGE EXTENSIONS OF GRASSES INTO COLORADO.¹ In connection with the preparation of a flora of Colorado many plants not listed for the state in the various manuals and monographs have come to light. Among these unrecorded plants are 32 grass species.

Because of the great economic importance of the grass family in this region, and because, as far as can be ascertained, the majority of these grasses are a part of the actual flora of the state, it was considered worth while to put them on record, together with the herbaria wherein the specimens are deposited. The following abbreviations are used: University of Colorado (CU); Colorado Agricultural and Mechanical College (CA); Colorado College (CC); United States Forest Service, Regional Office, Denver (FS); Rocky Mountain Forest and Range Experiment Station, Fort Collins (FES); private herbarium of Paul Ginter, Fort Collins (G); Soil Conservation Service, maintained by the Department of Range and Pasture Management, Colorado Agricultural and Mechanical College (SS); United States National

¹ Scientific Series Paper 216, Colorado Agricultural Experiment Station.

Museum (US); Rocky Mountain Herbarium, University of Wyoming (W).

I. Casual, perhaps cultivated, introductions:

1. *Anthoxanthum odoratum* L., CC, SS.
2. *Brachypodium distachyon* (L.) Beauv., CU.
3. *Bromus catharticus* Vahl., CA, W.
4. *Cynodon Dactylon* (L.) Pers. CA.
5. *Cynosurus cristatus* L., CC, SS.
6. *Eleusine indica* (L.) Gaertn., CA, FS.
8. *Muhlenbergia Schreberi* Gmel., CA.
9. *Paspalum racemosum* L., CU.
10. *Poa trivialis* L., CU.
11. *Zizania aquatica* var. *angustifolia* Hitchc., CC.

II. Native or well established grasses:

1. *Agropyron latiglume* (S. & S.) Rydb., FS.
2. *Aristida Curtissii* (A. Gray) Nash, CA.
3. *Aristida purpurea* Nutt., W.
4. *Bouteloua barbata* Lag., CA.
5. *Calamagrostis montanensis* (Scribn.) Scribn., CA.
6. *Calamovilfa gigantea* (Nutt.) Scribn. & Merr., CA, CC, FES, SS.
7. *Danthonia unispicata* (Thurb.) Munro, CA.
8. *Elymus salina* Jones, US.
9. *Eragrostis Barrelieri* Daveau., CA, SS.
10. *Eragrostis trichodes* (Nutt.) Wood, CA.
11. *Eriochloa contracta* Hitchc., CA, CU.
12. *Muhlenbergia arenacea* (Buckl.) Hitchc., CA.
13. *Panicum huachucae* Ashe, CA.
14. *Panicum Wilcoxianum* Vasey, FS, G.
15. *Paspalum stramineum* Nash, CA, W.
16. *Poa bulbosa* L., CA, FS, W.
17. *Poa scabrella* (Thurb.) Benth., CU.
18. *Sorghum halepense* (L.) Pers., CA.
19. *Sporobolus heterolepis* (Gray) Gray, CU, CA, SS, CC.
20. *Sporobolus neglectus* Nash, CA.
21. *Stipa spartea* Trin., CA, CC, W.

None of the above 32 grasses has been previously directly recorded for Colorado in the knowledge of the writer. All specimens considered doubtful were sent to the United States National Museum for determination.—H. D. HARRINGTON, Department of Botany and Plant Pathology, Colorado Agricultural and Mechanical College, Fort Collins, Colorado.